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Systematic and comparative anatomy of Maxillarieae (Orchidaceae), sans Oncidiinae

WILLIAM LOUIS STERN, WALTER S. JUD, and BARBARA S. CARLSWARD

Abstract

On the basis of floral and vegetative morphology, 63 tropical American genera have been recognized within Maxillarieae. We were able to examine anatomical material of all subtribes, excluding Oncidiinae. Stegmata with conical silica bodies occur in leaves and stems of all subtribes excluding Ornithocephalinae, and pericyclic stegmata found in roots are characteristic of Lycastinae. Lycastinae and Maxillariinae are characterized by foliar glands, foliar fibre bundles and tilosomes. Endodermal cells are U-thickened in most Zygopetalinae; O-thickened in most Lycastinae, Ornithocephalinae and Telipogoninae; variously thickened in Maxillariinae; and thin-walled in *Cryptarrhena lunata*. Water-storage cells varied from thin-walled to variously banded throughout Maxillarieae. Cladistic analyses using anatomical characters yielded no resolution among subtribes, illustrating that anatomical characters are of limited value in assessing relationships within this tribe.

Keywords: cladistic analysis, stegmata, tilosome, vegetative anatomy, velamen, water-storage cell

INTRODUCTION

Our study concerned the comparative anatomy and systematics of tribe Maxillarieae (Dressler, 1993), exclusive of Maxillaria and its relatives (Holtzmeier, Stern & Judd, 1998), and of subtribe Oncidiinae, both of which are very large groups within Maxillarieae that will be covered in later anatomical studies. We examined specimens of taxa available in subtribes Cryptarrheninae, Zygopetalinae, Lycastinae, Maxillariinae, Ornithocephalinae and Telipogoninae. Among these subtribes of Maxillarieae, Dressler (1993) recognized 63 genera. We have included two more recently described genera: *Ackermania* and *Chondroscaphe*. All these Maxillarieae are distributed in tropical America. We reviewed literature pertaining to studies of these groups only to find, for the most part, random observations on very few taxa, and no comprehensive treatments. Previous studies were mostly organ-based with little or no attempt to apply any systematic interpretation. Of those where brief mention of anatomy of our group was included, we note Leitgeb (1864), Krüger (1883), Moreau (1913), Löw (1926) and Oliviera & Sajo (1999). Of a somewhat more substantial nature are the papers of Möbius (1887) on leaves, Meinecke (1894) on aerial roots, Weltz (1897) and Hering (1900) on stems, Duruz (1960) on stomata, and Williams (1976) on subsidiary cell development. In each case only one or a few members of Maxillarieae were treated.

Möbius (1887) noted hairs on leaves of *Zygopetalum mackaii* Hook. f. and that these leaves differed from those of *Lycaste* by lacking fibre bundles. In *Lycaste* fibre

bundles were distributed between the vascular bundles, whereas in *Xylobium* they formed two rows, one above and one below the row of vascular bundles. Hairs were present on leaves of *Xylobium* and *Lycaste* but were lacking in *Scuticaria*. In the centric leaves of *Scuticaria* vascular bundles were organized in four concentric circles, and the outer margin of the leaf was characterized by fibre bundles reaching into the adaxial groove. The anatomy of *Chondrorhyncha* resembled that of *Zygopetalum*, but leaves in *Zygopetalum* showed a hypodermis that was absent in *Chondrorhyncha*. *Dichaea* lacked hairs and fibre bundles. Möbius remarked that he had very little material of these genera.

Meinecke (1894) reported on aerial roots, but appeared at least in part to be repeating the observations of Leitgeb (1864 , ' Leitgeb hat aus dieser Gruppe folgende Species geschildert .'). He noted the seriation of velamen in *Xylobium pallidiflorum* G. Nicholson (7), *X. squalens* Lindl. (8) , *Bifrenaria atropurpurea* Lindl. (10), *B. harrisoniae* (Hook. f.) Rchb. f. (7), *Lycaste tetragona* Lindl. (6), and *L. tricolor* Rchb. f. (7,8). He stated that the velamen wall next to the 'endodermis' (actually, exodermis) had 'complicated thickening ridges' above the small cells (passage cells?) in *Xylobium pallidiflorum* ; almost surely these were tilosomes. He also noted certain cortical parenchyma cells in *X. pallidiflorum* and *Bifrenaria atropurpurea* to be characterized by very fine arabesques, i.e. reticulate wall thickenings. Again, he noted 'thickening ridges' in *Zygopetalum crinitum* G. Nicholson. Meinecke included *Cochleanthes* (as *Warscewiczella*) in *Huntleyinae* and noted velamen layers as 4, 5. The vascular cylinder was 11-rayed, the elements being embedded in thick-walled cells, but the pith comprised unthickened parenchyma cells.

Weltz (1897) described epidermal cells of pseudobulbs in *Bifrenaria* and *Lycaste* as very thick-walled, short and rounded with a lenticular lumen. The walls had numerous simple pits with branched pit canals. Similarly, epidermal stem cells in *Xylobium squalens* were short with narrow lumina, had simple pits in the walls and branched pit canals. A sclerenchymatous hypodermis of 2 or 3 layers appeared in *Bifrenaria* and *Lycaste* and 4 or 5 layers in *Xylobium* . Ground tissue consisted of thin-walled parenchyma cells interspersed with intercellular spaces and with large lacunae in *Xylobium*. Vascular bundles were scattered, and in *Bifrenaria* and *Lycaste* there were both phloem and xylem sheaths associated with silica cells. The cauline epidermis of *Zygopetalum mackaii* possessed a thick cuticle, thick cell walls, a lenticular lumen and branched pit canals in cell walls. Ground tissue consisted of thin-walled larger and smaller cells, among which were intercellular spaces. Vascular bundles were very small, scattered and had only a phloem sheath with accumulated silica cells. Epidermal cells of the rhizome had only slightly thickened cell walls covered by a thin cuticle. Ground tissue contained 'rounded spiral fibre cells' in the outer layers; in the inner layers, however, these cells had elliptical pits. Collateral vascular bundles were scattered; the phloem sheath was well developed; but there were no silica cells.

Hering (1900) studied the stem of only *Dichaea vaginata* Rchb. f. The epidermis was covered by a thin, smooth cuticle. The endodermis (i.e. exodermis) consisted of

slightly elongated, anticlinally orientated cells. The underlying 1–3 layers of cells lacked intercellular spaces in spite of their parenchymatous form. There were no vascular bundles in the 6–8 layers immediately subtending the endodermis. The first vascular bundles to appear were organized as an irregular circle in the ground tissue and distributed internally so that no pith was formed. Vascular bundles increased in size from outer to inner regions of the stem. A sclerenchyma sheath was present at both xylem and phloem poles. Silica bodies occurred in cells neighbouring the sclerenchyma sheath and appeared as large biconvex discs.

Duruz (1960) described the leaf of *Zygopetalum crinitum* as thin and fibrous. The superficial stomata were distributed irregularly on the lower side of the lamina. Epidermal cells were polygonal and 5- or 6-sided and those surrounding the stoma were smaller than other epidermal cells. There were almost always four accessory cells bordering the stoma. Cuticle was equally thick (4 μm) along both leaf surfaces. Upper epidermal cells were wider (35 μm) than cells of the lower epidermis (21 μm). Cuticle covered the inside of the stomatal apparatus. Guard cells were provided with well-developed almost connivent outer horns leaving a very small space between them, thus protecting the leaf from desiccation by retarding transpiration. Internally, there was also a pair of cutinized horns. There was no front cavity and the substomatal chamber was medium sized. Mesophyll constituted rounded cells and the mid-vein extended from epidermis to epidermis.

In the leaf of *Zygopetalinae* (Williams, 1976) the guard cell mother cell of the nascent stomatal apparatus was shorter than other epidermal cells and was identifiable because of this. It was barrel-shaped, its cell walls were more refractive than those of other epidermal cells and the nucleus was more deeply staining. The final division of the guard cell mother cell resulted in the two guard cells. Mature subsidiary cells, however, were derivatives of the trapezoidal cells, which themselves resulted from oblique divisions in the neighbouring cells. This process resulted in the tetracytic stomatal organization with four subsidiary cells. Williams stated that no species of *Zygopetalinae* had been found to lack distinct subsidiary cells. Among *Zygopetalinae* only two species had amphistomatal leaves; all other species showed hypostomatal leaves. He suggested that more advanced genera, such as found in *Zygopetalinae*, seemed to have distinct subsidiary cells that were derivatives of trapezoid cells.

MATERIAL AND METHODS

Specimens on which this study is based are listed alphabetically with associated binomials, authorities and parts available for study under their respective subtribes in Table 1. We had available for study representatives of 43 of the 63 genera listed under *Maxillarieae* by Dressler (1993), plus specimens of two genera he did not list. In total, we looked at 127 species, usually represented by a single specimen. Where genera in our collection were represented by multiple species, a single species from that group was selected for detailed study. Individual observations, then, were verified by comparing them with those of other species in the group. Because of

their large size, members of the genus *Maxillaria* and subtribe *Oncidiinae* were not included in this study but will be included in later anatomical studies. Abbreviations of authors for binomials follow the recommendations of Brummitt & Powell (1992). Vouchers are represented by preserved specimens in FLAS, although some are vouchered at K. Methods and descriptive conventions have appeared in recently published papers (Stern & Judd, 2001, 2002; Yukawa & Stern, 2002) and we have followed similar procedures here. However, we did not describe stem structure for those genera with a flabellate, or fan-shaped habit, such as *Cochleanthes*, *Bollea* and *Ornithocephalus*. In these, stems are so foreshortened, the internodes so compressed, the vascular traces so tortuous as to make clear interpretations impractical, if not impossible.

Table 1. Species of Maxillarieae studied. L, leaf; S, stem; R, root

Taxa	Parts available	Taxa	Parts available
<i>Cryptarrheninae</i>		<i>Dichaea verrucosa</i> Ames & C. Schweinf.	L, R
<i>Cryptarrhena guatemalensis</i> Schltr.	L, S	<i>Galeottia fimbriata</i> (Linden & Rchb. f.) Schltr. 1706	L, S, R
<i>Cryptarrhena lunata</i> R. Br.	L, R	<i>Galeottia fimbriata</i> 1723	L, S
<i>Zygopetalinae</i>		<i>Galeottia grandiflora</i> A. Rich. & Galeotti	L, S, R
<i>Ackermania caudata</i> (Ackerman) Dodson & R. Escobar	L, R	<i>Galeottia negrensis</i> Schltr. 1699	L, R
<i>Ackermania cornuta</i> (Garay) Dodson & R. Escobar	L, R	<i>Galeottia negrensis</i> 1741	S
		<i>Huntleya heteroclita</i> (Poepp. & Endl.) Garay	L, R
<i>Aganisia</i> sp.	L, S, R	<i>Huntleya meleagris</i> Lindl.	R
<i>Aganisia cyanea</i> Benth. & Hook. f.	L, S, R	<i>Kefersteinia</i> sp. 1749	L, R
<i>Batemanian</i> sp.	L, S, R	<i>Kefersteinia graminea</i> Rchb. f.	L, R
<i>Batemanian ciliata</i> (J. M. Morel) Cogn.	L, S, R	<i>Kefersteinia lactea</i> (Rchb. f.) Schltr.	L, R
<i>Batemanian colleyi</i> Lindl.	L, S, R	<i>Kefersteinia maculosa</i> Dressler	L, R
<i>Bollea violacea</i> Rchb. f. 1679	L, R	<i>Kefersteinia mystacina</i> Rchb. f.	L, R
<i>Bollea violacea</i> 112	L, R	<i>Kefersteinia tolimensis</i> Schltr.	L, R
<i>Chaubardia heteroclita</i> (Poepp. & Endl.) Dodson & D. E. Benn.	L, R	<i>Koellensteinia altissima</i> Pabst 1101	L
<i>Chaubardia klugii</i> (C. Schweinf.) Garay 1700	L, R	<i>Koellensteinia altissima</i> 1695	L, R
<i>Chaubardia klugii</i> 1709	L, R	<i>Koellensteinia carraoensis</i> Garay & Dunst.	R
<i>Chaubardiella chasmatochila</i> (Fowlie) Garay	L, R	<i>Koellensteinia graminea</i> Rchb. f.	L, R
<i>Chaubardiella dalessandroi</i> Dodson & Dalström	L, R	<i>Neogardneria murrayana</i> Schltr. 282	L, S, R
		<i>Neogardneria murrayana</i> 502	L, S
		<i>Otostylis lepida</i> Schltr.	L, S, R
<i>Chondrorhyncha</i> sp. 1693	L, R	<i>Pabstia viridis</i> (Lindl.) Garay	L, R
<i>Chondrorhyncha amabilis</i> Schltr. 1729	R	<i>Paradisianthus micranthus</i> (Barb. Rod.) Schltr.	R
<i>Chondrorhyncha andreae</i> P. Ortiz 1697	L		
<i>Chondrorhyncha andreae</i> 1746	L, R	<i>Pescatoria cerina</i> Rchb. f.	L, R
<i>Chondrorhyncha andreettae</i> Jenny	L, R	<i>Pescatoria dayana</i> Rchb. f.	L, R
<i>Chondrorhyncha carinata</i> P. Ortiz	L	<i>Pescatoria klabochorum</i> Rchb. f.	L, R
<i>Chondrorhyncha chestertonii</i> Rchb. f.	L, R	<i>Promenaea lentiginosa</i> (Lindl.) Lindl.	L, S, R

<i>Chondrorhyncha hirtzii</i> Dodson	L, R	<i>Promenaea xanthina</i> Lindl. [‡]	L, S, R
<i>Chondrorhyncha lodyana</i> Rchb. f.	L, R	<i>Scuticaria hadwenii</i> (Lindl.) Hoehne	L, R
<i>Chondrorhyncha reichenbachiana</i> Schltr.	R	<i>Stenia guttata</i> Rchb. f.	L, R
<i>Chondroscaphe escobariana</i> (Dodson & Neudecker) G. S. Ringius	L, R	<i>Stenia pallida</i> Lindl. 1688	L, R
		<i>Stenia pallida</i> 1705	L, R
<i>Cochleanthes amazonica</i> (Rchb. f. & Warscz.) R. E. Schult. & Garay	L, R	<i>Warrea warreana</i> (Lodd. ex Lindl.) C. Schweinf. 508	L, S
<i>Cochleanthes aromatica</i> (Rchb. f.) R. E. Schult. & Garay	L, R	<i>Warrea warreana</i> 1698	L, R
		<i>Warrea warreana</i> 1479	L, S, R
<i>Cochleanthes discolor</i> (Lindl.) R. E. Schult. & Garay 604	L, R	<i>Zygopetalum crinitum</i> Lodd.	L, S, R
		<i>Zygopetalum intermedium</i> Lodd. [‡]	L, R
<i>Cochleanthes discolor</i> [‡]	L, R	<i>Zygopetalum mackaii</i> Hook. f. 1483	R
<i>Cochleanthes flabelliformis</i> (Sw.) R. E. Schult. & Garay	L, R	<i>Zygopetalum mackaii</i> 1760	L, R
		<i>Zygosepalum labiosum</i> (Rich.) C. Schweinf.	L, S, R
<i>Cochleanthes marginata</i> (Rchb. f.) R. E. Schult. & Garay 1678	L, R	<i>Zygosepalum lindeniae</i> (Rolfe) Garay & Dunst. Lycastinae	L, S, R
<i>Cochleanthes marginata</i> 1691	L, R	<i>Anguloa clowesii</i> Lindl.	L, S
<i>Dichaea camaridoides</i> Schltr.	L, S, R	<i>Anguloa ruckeri</i> Lindl.	R
<i>Dichaea chasei</i> Dodson	L, S, R	<i>Anguloa uniflora</i> Ruiz & Pav.	L, S, R
<i>Dichaea hystricina</i> Rchb. f.	L	<i>Anguloa virginalis</i> Linden ex Schltr.	L, S
<i>Dichaea longa</i> Schltr.	L, S	<i>Anguloa virginalis</i> [‡]	L, S
<i>Dichaea muricata</i> Lindl. [‡]	L, R	<i>Bifrenaria harrisoniae</i> (Hook. f.) Rchb. f.	L, S, R
<i>Dichaea trulla</i> Rchb. f.	L, R	<i>Bifrenaria inodora</i> Lindl.	L, R
<i>Bifrenaria minuta</i> Garay [‡]	L	<i>Xylobium variegatum</i> 1066	L, S
<i>Bifrenaria tetragona</i> (Lindl.) Schltr.	R	<i>Xylobium variegatum</i> 1276	R
<i>Bifrenaria tyrianthina</i> Rchb. f. 341	L, R	Maxillariinae	
<i>Bifrenaria tyrianthina</i> 1116	S	<i>Anthosiphon roseans</i> Schltr.	L
<i>Bifrenaria tyrianthina</i> 1761	L	<i>Cryptocentrum gracillimum</i> Ames & C. Schweinf.	L
<i>Bifrenaria wendlandiana</i> Cogn.	R	<i>Cryptocentrum gracilipes</i> Schltr.	R
<i>Lycaste aromatica</i> Lindl. 857	L	<i>Cyrtiodorchis frontinoensis</i> (Garay) S. Rauschert	L, R
<i>Lycaste aromatica</i> 1188	R	Ornithocephalinae	
<i>Lycaste brevispatha</i> Klotzsch ex Rchb. f.	L, S, R	<i>Dipteranthus planifolius</i> (Rchb. f.) Garay	L, S, R
<i>Lycaste campbellii</i> C. Schweinf.	L, S	<i>Hintonella mexicana</i> Ames	L, R
<i>Lycaste ciliata</i> (Ruiz & Pav.) H. J. Veitch	L, S	<i>Ornithocephalus bicornis</i> Lindl.	L
<i>Lycaste consobrina</i> Rchb. f.	L	<i>Ornithocephalus cochleariformis</i> C. Schweinf.	R
<i>Lycaste cruenta</i> Lindl.	R	<i>Ornithocephalus dolabratus</i> Rchb. f. 1676	L
<i>Lycaste deppei</i> Lindl.	L, R	<i>Ornithocephalus dolabratus</i> 1739	L, R
<i>Lycaste dowiana</i> Endres & Rchb. f.	L, S	<i>Ornithocephalus gladiatus</i> Hook. f.	L
<i>Lycaste fulvescens</i> Hook. f.	L, S	<i>Ornithocephalus inflexus</i> Lindl. 1596	L, R
<i>Lycaste macrobulbon</i> Lindl.	L, R	<i>Ornithocephalus inflexus</i> 1675	L, R
<i>Lycaste macrophylla</i> Lindl.	R	<i>Ornithocephalus iridifolius</i> Rchb. f.	L
<i>Lycaste suaveolens</i> Summerh.	L, S, R	<i>Phymatidium tillandsioides</i> Rodr.	L, S, R
<i>Lycaste xitriophora</i> Linden & Rchb. f.	R	<i>Sphyrastylis</i> sp. 1682	L, R
<i>Neomoorea wallisii</i> Schltr. 1476	L, S, R		
<i>Neomoorea wallisii</i> 1674	L		

<i>Neomoorea wallisi</i> [‡]	L, R	<i>Sphyrastylis ecuadorensis</i> Garay	L, R
<i>Rudolfiella floribunda</i> (Schltr.) Hoehne	L, S, R	<i>Sphyrastylis escobariana</i> Garay	L, R
<i>Rudolfiella saxicola</i> (Schltr.) Hoehne	L, R	<i>Sphyrastylis urceolabris</i> P. Ortiz & R. Escobar	L, R
<i>Stenocoryne aureofulva</i> (Hook. f.) Kraenzl.	L, S, R	1730	
<i>Stenocoryne vitellina</i> (Lindl.) Kraenzl.	L, S, R	<i>Sphyrastylis urceolabris</i> 1719	L, R
<i>Teuscheria dodsonii</i> Dressler	L, R	<i>Zygostates alleniana</i> Kraenzl.	L, R
<i>Xylobium colleyi</i> Rolfe	L, S, R	Telipogoninae	
<i>Xylobium foveatum</i> (Lindl.) G. Nicholson	L, S, R	<i>Stellilabium</i> sp.	L, R
<i>Xylobium leontoglossum</i> Rolfe 1438	L, S	<i>Telipogon pulcher</i> Rchb. f.	L, R
<i>Xylobium leontoglossum</i> [‡]	L, R	<i>Trichoceros tupaipi</i> Rchb. f.	L
<i>Xylobium palmifolium</i> (Sw.) Fawc.	L, S, R	<i>Trichoceros antennifer</i> Humb. Bonpl. & Kunth	L, R
<i>Xylobium variegatum</i> (Ruiz & Pav.) Garay & Dunst. 1757	L, S, R		

* These are the first author's catalogue numbers and are used here to differentiate between two or more specimens of the same species.

† Kew microscope slide.

As a shorthand in descriptions, instead of 'periclinally orientated' and 'anticlinally orientated', we have just noted 'periclinal' and 'anticlinal'. We have omitted most verbs except where they are essential for clarity.

Plant parts were preserved in FAA (9 parts 70% ethanol, 0.5 parts glacial acetic acid and 0.5 parts commercial formalin) and stored in 70% ethanol. Transverse and longitudinal sections of leaves and transverse sections of stems and roots were cut as thinly as possible with a Reichert sliding microtome, stained in Heidenhain's iron-alum haematoxylin, and counter-stained with safranin. Leaf scrapings followed Cutler's (1978) methods and were stained with safranin. Leaves too delicate to scrape successfully were cleared in 5% aqueous sodium hydroxide, washed in running water, treated with Stockwell's solution, washed in running water again and stained with safranin. Sections, scrapings and clearings were mounted on glass slides using Canada balsam. Observations were made using a Nikon Optiphot microscope, and pictures were taken with an Olympus BH-2 Epifluorescent Microscope system and a Pixera 120C digital camera. Measurements of the lengths and widths of ten guard-cell pairs were made and these are given in Table 2. Utilizing a Hitachi S-4000 instrument, scanning electron micrographs were prepared from selected species for recording tilosome features. Because it is questionable if tilosome features can be discerned finely enough with the light microscope, even with the oil-immersion lens, tilosomes were recorded only as present or absent, except for those viewed from SEM photomicrographs. Transverse sections of roots were made from material preserved in FAA and stored in 70% ethanol. These were placed in mesh bags and dehydrated through an ethanol series into absolute alcohol. Mesh bags were placed into the critical point dryer; processed, and placed on acetone-cleaned aluminium stubs using graphite tabs. Stubs containing samples to be viewed were placed into the specimen chamber of the SEM. Pictures were recorded by computer using the Spectrum Mono program.

Table 2. Stomatal dimensions (µm)

Taxon	Average		Range	
	Length	Width	Length	Width
Cryptarrheninae				
<i>Cryptarrhena guatemalensis</i>	44	33	37–52	27–42
Zygopetalinae				
<i>Ackermania caudata</i>	41	38	37–45	27–45
<i>Ackermania cornuta</i>	39	36	37–42	32–40
<i>Aganisia</i> sp.	36	32	35–40	30–37
<i>Batemanianthus colleyi</i>	37	32	35–40	27–37
<i>Bollea violacea</i>	49	40	42–52	35–40
<i>Chaubardia klugii</i> 1700	37	32	32–40	32–35
<i>Chaubardiella dalessandroi</i>	37	34	32–42	27–35
<i>Chondrorhyncha lendyana</i>	40	36	35–47	27–42
<i>Chondroscaphe escobariana</i>	34	35	30–36	32–40
<i>Cochleanthes aromatica</i>	42	29	37–45	27–30
<i>Dichaea muricata</i>	34	29	30–37	25–35
<i>Galeottia fimbriata</i> 1723	41	34	37–47	32–37
<i>Huntleya heteroclita</i>	49	37	45–52	30–45
<i>Kefersteinia</i> sp. 1749	36	30	25–40	25–35
<i>Koellensteinia altissima</i>	44	37	40–47	35–40
<i>Neogardneria murrayana</i>	36	33	32–42	30–37
<i>Otostylis lepida</i>	36	35	32–45	30–42
<i>Pabstia viridis</i>	51	32	47–55	27–40
<i>Pescatoria cerina</i>	45	37	42–50	35–40
<i>Promenaea xanthina</i>	39	31	32–42	27–37
<i>Scuticaria hadwenii</i>	–	–	–	–
<i>Stenia pallida</i> 1705	41	39	37–42	32–45
<i>Warrea warreana</i> 508	43	40	37–55	32–40
<i>Zygopetalum crinitum</i>	48	35	42–55	27–40
<i>Zygosepalum lindeniae</i>	35	27	32–37	25–30
Lycastinae				
<i>Anguloa virginialis</i>	36	30	32–37	25–35
<i>Bifrenaria harrissoniae</i>	50	54	47–55	47–60
<i>Lycaste aromatica</i> 857	42	32	37–47	27–37
<i>Neomoorea wallisii</i> 1476	34	30	32–37	27–35
<i>Rudolfiella floribunda</i>	46	48	42–52	45–50
<i>Stenocoryne vitellina</i>	47	41	42–52	35–45
<i>Teuscheria dodsonii</i>	30	26	30/30	25–27
<i>Xylobium variegatum</i> 1066	36	34	30–40	30–37
Maxillariinae				
<i>Anthosiphon roseans</i>	36	24	32–40	25–30
<i>Cryptocentrum gracillimum</i>				
adaxial	47	40	42–50	37–47
abaxial	50	39	47–52	35–42

<i>Cyrtidiorchis frontinoensis</i>	42	34	32–50	32–37
Ornithocephalinae				
<i>Dipteranthus planifolius</i>	44	37	42–50	32–40
<i>Hintonella mexicana</i>	42	36	37–45	32–40
<i>Ornithocephalus gladiatus</i> 1734	50	51	47–57	45–57
<i>Phymatidium tillandsioides</i>	–	–	–	–
<i>Sphyrastylis ecuadorensis</i>	48	37	42–50	32–42
<i>Zygostates alleniana</i>	–	–	–	–
Telipogoninae				
<i>Stellilabium</i> sp.	–	–	–	–
<i>Telipogon pulcher</i>	49	37	42–60	30–40
<i>Trichoceros tupaipi</i>	56	49	55–60	42–52

Eight features of the anatomy of leaf, pseudobulb and root were used to construct the character matrix for cladistic analysis of genera in Maxillarieae as delineated here (Tables 3, 4). Cladistic analyses were performed using the computer program HENNIG86 (Farris, 1988), generating trees by a heuristic strategy involving the addition of terminals in random sequence, producing many trees, to each of which extended branch-swapping is applied (mhennig*; bb*) and by implicit enumeration (ie-) with extended branch swapping (bb*). Trees were rooted using *Dipteranthus* and *Ornithocephalus* of the Ornithocephalinae, and *Telipogon* and *Trichoceros* of the Telipogoninae as outgroups. This rooting is supported by recent DNA-based phylogenetic analyses (Cameron et al., 1999; Williams et al., 2001), which support the placement of genera of Ornithocephalinae and Telipogoninae within an expanded Oncidiinae (Williams, Whitten & Chase, 1999). The Oncidiinae are probably sister to a large clade containing Zygopetalinae (including Cryptarrhena), Maxillariinae (including Lycastinae), and Stanhopeinae, along with a few other genera (Williams et al., 1999). Thus *Dipteranthus*, *Ornithocephalus*, *Telipogon* and *Trichoceros* can appropriately function as outgroups in these analyses of generic relationships within and among Cryptarrheninae, Zygopetalinae, Lycastinae and Maxillariinae.

Table 3. Anatomical characters used in cladistic analysis of Maxillarieae. Presumed plesiomorphic states are listed first (0), followed by apomorphic ones (1, 2). Polarization assumes rooting with Ornithocephalinae and Telipogoninae (as functional outgroups); see text. Where character state varies among outgroup taxa, the majority state (in outgroup taxa) is arbitrarily coded as ‘0’

No.	Anatomical character
1	Foliar water-storage cells present (0), absent (1).
2	Stegmata in leaf absent (0), present (1).
3	Stegmata in root absent (0), present (1).
4	Tilosomes absent (0), present (1).

5	Foliar glands absent (0), present (1).
6	Foliar fibre bundles absent (0), present (1).
7	Endodermal cell wall thickenings O-thickened (0), u-thickened (1), thin (2).
8	Pseudobulbs present (0), absent (1).

Table 4. Character state values for genera used in cladistic analysis

Genus	Character							
	1	2	3	4	5	6	7	8
<i>Cryptarrhena</i>	0/1	1	0	0	0	0	2	0/1
<i>Ackermania</i> [*]	0	1	0	0	0	0	1	1
<i>Galeottia</i> [†]	0	1	0	0	0	0	1	0
<i>Aganisia</i> [‡]	1	1	0	0	0	0	1	0
<i>Bollea</i>	0	1	0	0	0	0	0	1
<i>Batemanina</i>	0	1	?	0	0	0	1	0
<i>Chondroscaphe</i>	0	1	0	0	0	0	1	1
<i>Neogardneria</i>	1	1	0	0	0	0	1	0
<i>Kefersteinia</i>	0/1	1	0	0	0	0	1	1
<i>Zygosepalum</i>	0	1	0	0	0	0	1	0
<i>Koellensteinia</i>	0/1	1	0	0	0	1	0	0
<i>Otostylis</i>	1	1	0	0	0	1	1	0
<i>Scuticaria</i>	0	1	0	0	0	1	1	0
<i>Warrea</i>	1	1	0	0	0	0	0	0
<i>Zygopetalum</i>	0	1	0	0	0	0/1	1	0
<i>Anguloa</i> [§]	0/1	1	1	1	1	1	0	0
<i>Lycaste</i>	1	1	1	1	1	1	0	0
<i>Rudolfiella</i>	1	1	0	0	1	1	0/2	0
<i>Stenocoryne</i>	1	1	1	0	1	1	0	0
<i>Teuscheria</i>	1	1	0	0	1	1	1	0
<i>Cryptocentrum</i>	0	1	0	1	1	1	0	0
<i>Cryptidiorchis</i>	0	0	0	1	1	0	1	0
Functional outgroups								
<i>Dipteranthus</i> ^{**}	0	0	0	0	0	0	0	0
<i>Orhithocephalus</i> ^{††}	0	0	0	0	0	0	0	1
<i>Telipogon</i>	0	1	0	0	0	0	0	1
<i>Trichoceros</i>	0	1	0	0	0	0	0	0

* The following genera have the same character states as *Ackermania*: *Chaubardia*, *Chaubardiella*, *Chondrorhyncha*, *Cochleanthes*, *Dichaea*, *Huntleya*, *Pescatoria* and *Stenia*.

† *Promenaea* has identical character state codings.

‡ *Pabstia* has identical character state codings.

§ *Bifrenaria* and *Xylobium* have identical character state codings.

|| *Neomoorea* has identical character state codings.

** *Hintonella* has identical character state codings.

†† *Sphyrastylis* and *Zygostates* have identical character state codings.

All characters were readily divisible into discrete states, thus avoiding arbitrary decisions in state delimitation. Features excluded from the cladistic analyses because discrete states could not easily be delimited included stomatal size, cuticle thickness, pattern of fibre bundles associated with vascular tissues of leaves and stems, number of velamen layers and number of xylem/phloem groups in roots. The presence or absence of branched bars in foliar water-storage cells was not used as a phylogenetic character because it often varies infragenerically, e.g. in *Batemanina*, *Bifrenaria*, *Chondrorhyncha* and *Ornithocephalus*. Many anatomical features were too uniform within this group of genera to be of much phylogenetic value (see taxon descriptions). Multistate characters were considered unordered and character codings are presented in Tables 3 and 4. Infrataxon variable characters were analysed as missing data.

ANATOMY

In transverse section, the cortices of roots in almost all species examined consist of two kinds of cells: typical thin-walled, more or less circular parenchyma cells that may have banded, branched secondary wall thickenings, and idioblasts with angular outlines whose walls are more or less thickened and that refract polarized light (Fig. 1). These cells are empty, lacking both nucleus and cytoplasm. They are solitary cells scattered about the cortex, but often concentrated near the exodermis. We had an opportunity to examine these cells in longitudinal section for *Promenaea xanthina*, *Zygopetalum intermedium*, *Dichaea muricata*, *Xylobium leontoglossum*, *Lycaste aromatica* and *Neomoorea wallisii*.

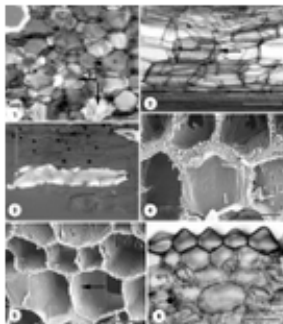


Figure 1–6. Fig. 1. *Aganisia cyanea* . T-S root cortex with birefringent idioblasts (arrows) and normal assimilatory cells (arrowhead). Scale bar = 100 μ m. Fig. 2. *Promenaea xanthina* . L-S root cortex showing isotropic, inflated idioblasts (arrow). Scale bar = 100 μ m. Fig. 3. *Lycaste aromatica* . L-S root cortex with birefringent, elongated idioblasts. Scale bar = 100 μ m. Fig. 4. *Anguloa ruckeri* . SEM velamen showing lamellate tilosomes. Scale bar = 23 μ m. Fig. 5. *Cryptarrhena lunata* . SEM velamen with spiral wall thickenings and exodermal cells with ladder-like wall thickenings (arrow). Scale bar = 27 μ m. Fig. 6. *Ackermania caudata* . T-S papillate foliar epidermis. Scale bar = 100 μ m.

In longitudinal section, cells are elongated in *Promenaea xanthina* (Fig. 2), sometimes barrel-shaped, the walls are red-staining (safranin) and have elliptical pits perpendicular to the long axis of the cells. Cells are slightly thick-walled and isotropic, i.e. non-birefringent. In *Zygopetalum intermedium*, idioblasts are elongated with thickened, birefringent cell walls, but they lack lateral wall pitting. In *Xylobium leontoglossum*, cells are elongated with somewhat thickened, birefringent walls. Elongated idioblasts of *Lycaste aromatica* are of various lengths, very thick-walled with a scalloped outline, fusiform (Fig. 3). There were no pits in the walls. Idioblasts of *Neomoorea wallisii* resembled those of *Lycaste aromatica*, but cell walls were thinner. Owing to their lack of contents it is tempting to call these idioblasts water-storage cells, but because of the lack of evidence, their elongated

form and sometimes thick walls, we think it best at the time of writing to delay assigning this function to them.

All leaves seen are hypostomatic, but there are always a few adaxial stomata. In many instances, the polar and lateral subsidiary cells of stomatal apparatuses are divided once or more, betraying the fundamental tetracytic configuration that is widespread in Maxillarieae group. Leaves are mostly planate, but they are terete in Scuticaria. In subtribe Ornithocephalinae, leaves may be called isobilateral, centric, unifacial or even cylindrical. As noted in the Material and methods section, tilosomes are characteristic of certain genera, but we hesitate to classify them without viewing with the SEM. The light microscope does not show tilosome detail sufficient to characterize them. We did, however, examine several species for the presence or absence of tilosomes with the SEM and we were able to characterize them in several species where they were present: tilosomes are lamellate in Anguloa (Fig. 4) and Lycaste and probably so in Cyrtidiorchis. Otostylis, Warrea, Stenia, Cryptarrhena and Stenocoryne lack these structures.

Cryptarrheninae

Leaf

Surface. hairs sunken, adaxial only. stomata abaxial, tetracytic, subsidiary cells sometimes divided. Adaxial and abaxial epidermal cells polygonal, adaxial cell walls straight-sided, abaxial cell walls curvilinear.

Section. cuticle smooth, adaxial and abaxial, about 2.5 μm thick. epidermal cells on both surfaces isodiametric and periclinal, variably shaped. stomata superficial; substomatal chamber smaller than adjacent mesophyll cells in Cryptarrhena lunata, larger in Cryptarrhena guatemalensis. Outer ledges moderate, inner ledges obscure, margins of subsidiary cells rounded internally. fibre bundles absent. mesophyll homogeneous, 6 or 7 in Cryptarrhena guatemalensis or 10 cells wide in Cryptarrhena lunata. Cells very thin-walled, rectangular with rounded margins elongated parallel with epidermises in T-S. Crystalliferous idioblasts very thin-walled, circular in T-S, elongated, blunt-ended in L-S. Cells with widely spaced banded secondary cell wall thickenings. vascular bundles collateral in one series. Sclerenchyma thin-walled, mostly phloic, occasionally xylic in Cryptarrhena guatemalensis. stigmata with conical silica bodies always on phloem side, occasionally on xylem side in Cryptarrhena guatemalensis; in Cryptarrhena lunata, silica bodies poorly formed, sporadic in phloem side stigmata. Bundle sheath cells absent.

Stem

hairs and stomata absent. cuticle smooth, thin, somewhat more than 2.5 μm thick. epidermal cell walls greatly C-thickened on cuticle side, very thin-walled on inner surface. Cortex, endodermis and pericycle absent. ground tissue cells variably

shaped, thin-walled, mostly homogeneously sized, some empty, others packed with cruciate starch grains; intercellular spaces small, triangular. vascular bundles collateral, scattered, numerous. Thin-walled sclerenchyma associated only with phloem. stigmata with conical silica bodies phloic only.

Root

velamen 3- or 4-seriate, epivelamen cells periclinal, endovelamen cells mostly isodiametric; spiral thickenings with branched bars (Fig. 5); hairs unicellular. tilosomes absent. exodermal cells rectangular/polygonal, thin-walled, walls slightly thickened externally; passage cells intermittent with large nuclei. cortex 8 or 9 cells wide; cells thin-walled, circular to oval with chloroplasts throughout, some cells angular, thick-walled with birefringent walls lacking contents; intercellular spaces triangular. endodermis uniseriate, cells thin-walled, mostly periclinal, some isodiametric. pericycle as endodermis, but most cells isodiametric to slightly periclinal. vascular cylinder 11-arch with radial groups of xylem alternating with elliptical to circular clusters of phloem cells. Vascular tissue embedded in sclerenchyma. pith cells with thickened walls, mostly circular to polygonal with triangular intercellular spaces. Raphides in circular cortical cells.

Zygopetalinae

Leaf

Surface. hairs . Basal cell sunken, uniseriate. stomata abaxial, tetracytic, subsidiary cells frequently divided. Adaxial and abaxial epidermal cells polygonal, isodiametric and/or often elongated parallel with the veins on one or both surfaces, walls straight-sided or curvilinear.

Section. cuticle smooth, more or less 2.5 μm thick along both surfaces in most taxa, except adaxial up to 5.0 μm in *Chaubardiella dalessandroi* , *Chondroscaphe escobariana* and *Koellensteinia altissima* ; 5.0–7.5 μm in *Zygopetalum* ; 7.0–7.5 μm in *Chaubardia klugii* , *Dichaea muricata* , *Huntleya heteroclita* and *Otostylis lepida* ; 25.0 μm in *Scuticaria hadwenii* . epidermal cells more or less papillate in *Ackermania* (Fig. 6), isodiametric and periclinal in most taxa, outer walls thickened, conspicuously so in *Scuticaria hadwenii* . Substomatal chambers mostly small, i.e. not exceeding in size adjacent cells of the mesophyll, but in terete leaves of *Scuticaria* , substomatal chambers elongate, parallel to upright cells of mesophyll and may be wider or narrower than these cells (Fig. 7). Outer ledges small to moderate, moderate to large in *Chaubardiella dalessandroi* ; inner ledges obscure to apiculate, except pronounced and characterized by prominent cuticular 'horn' in *Scuticaria hadwenii* . fibre bundles absent in most taxa, present adaxially and abaxially alternating with vascular bundles in *Koellensteinia altissima* , adaxially and abaxially close to the epidermises in *Otostylis lepida* , sparse but alternating with vascular bundles in *Zygopetalum crinitum* and *Zygopetalum intermedium* , absent in *Zygopetalum mackaii* . In *Scuticaria hadwenii* , fibre bundles form a ring in

the outer layers of the leaf consisting of two series: a regularly organized outermost series and an intermittent inner series. Fibre bundles absent in the centre of the leaf. hypodermis abaxial, discontinuous, cells smaller than those of mesophyll in *Koellensteinia altissima*. mesophyll homogeneous, mostly narrow, 5–13 cells wide; heterogeneous in *Scuticaria hadwenii* where two layers of thin-walled chlorophyllous upright cells surround the periphery of the leaf, but this organization is not carried into the foliar groove. Centre of the leaf occupied by two kinds of cells: (1) oval and circular, thin-walled, chloroplast-containing cells with isotropic walls and (2) angular, thicker-walled, empty cells with birefringent walls. Triangular intercellular spaces dispersed among mesophyll cells. Primary pit fields of variable size and form. In taxa with a homogeneous mesophyll, cells crowded, usually thin-walled, circular but mostly oval, elongated parallel with the epidermises, and with few intercellular spaces as viewed in transverse section. In some cases mesophyll cells packed with cruciate starch grains. Crystalliferous idioblasts thin-walled and circular in transverse section and elongated, saccate, blunt-ended in longitudinal section. Various rotund water-storage cells with birefringent walls (Fig. 8) and sometimes bands of secondary wall thickenings differentially abundant scattered throughout the mesophyll (Fig. 9 ; Table 5). Primary pit fields vary in size and form. vascular bundles collateral in one series, except *Scuticaria hadwenii* where bundles are arranged in bilaterally symmetrical concentric circles centred on the foliar groove. The central circle consists of ten bundles, five on either side of the groove, plus a median bundle at the base of the groove. These are the largest bundles; small bundles in rings peripheral to these. All *Scuticaria* bundles collateral with abaxial phloem. Midveins usually have only a single abaxially positioned central vascular bundle, but this may be attended by two or more lateral, supernumerary bundles in *Ackermania cornuta* , *Aganisia cyanea* , *Batemaniania* sp., *Chondroscaphe escobariana* , *Huntleya heteroclita* , *Otostylis lepida* and *Warrea warreana* . Sclerenchyma usually ‘caps’ both xylem and phloem; it is absent in the smallest bundles or diminished at the xylem pole. Sclerenchyma is always more robust at the phloem pole than at the xylem pole. All *Zygopetalinae* have stegmata with conical, rough-surfaced silica bodies associated with foliar vascular bundle sclerenchyma. Stegmata appear to be absent next to xylem in smallest bundles of *Chondroscaphe escobariana* , *Koellensteinia altissima* and *Stenia pallida* . Stegmata with conical silica bodies accompany fibre bundles in *Koellensteinia altissima* , *Otostylis lepida* , *Zygopetalum c rinitum* , *Zygopetalum intermedium* and *Scuticaria hadwenii* . Bundle sheaths generally not well defined or absent; cells thin-walled, usually contain chloroplasts, and sometimes cruciate starch grains. Contrastingly, those of *Scuticaria hadwenii* are sharply delineated.

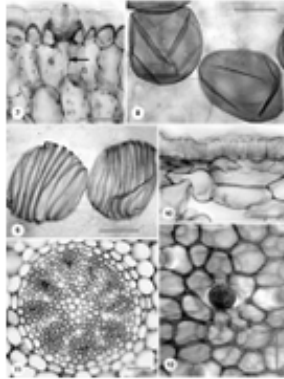


Figure 7–12. Fig. 7. *Scuticaria hadwenii*. T-S centric leaf depicting elongated substomatal chamber (arrow). Scale bar = 50 μ m. Fig. 8. *Chaubardia klugii*. Leaf scraping to show plain-walled, inflated water-storage cells. Scale bar = 50 μ m. Fig. 9. *Pescatoria cerina*. Leaf scraping illustrating water-storage cells with banded secondary wall thickenings. Scale bar = 50 μ m. Fig. 10. *Promenaea xanthina*. T-S pseudobulb showing epidermal cells with thickened outer and lateral walls and thin inner walls; note lenticular cell cavity. Scale bar = 50 μ m. Fig. 11. *Promenaea xanthina*. T-S vascular cylinder with U-thickened endodermal cell walls (arrow) opposite phloem clusters. Scale bar = 50 μ m. Fig. 12. *Xylobium colleyi*. Leaf scraping to show glandular hair in face view. Scale bar = 50 μ m.

Table 5. Foliar water-storage cells

Species	Plain	With branched bars	Species	Plain	With branched bars
Cryptarrheninae			<i>maculosa</i>	absent	
<i>Cryptarrhena</i>			<i>tolimensis</i>	absent	
<i>guatemalensis</i>	absent		<i>Koellensteinia</i>		
<i>lunata</i>		+	<i>altissima</i>	+	
Zygopetalinae			<i>graminea</i>	+	
<i>Ackermania</i>			<i>Neogardneria</i>		
<i>caudata</i>	+		<i>murryana</i>	absent	
<i>cornuta</i>	+		<i>Otostylis</i>		
<i>Aganisia</i>			<i>lepida</i>	absent	
sp.	absent		<i>Pabstia</i>		
<i>cyanea</i>	absent		<i>viridis</i>	absent	
<i>Batemanina</i>			<i>Pescatoria</i>		
sp.		+	<i>cerina</i>		+
<i>ciliata</i>	+		<i>dayana</i>		+
<i>colleyi</i>		+	<i>klabochozum</i>		+
<i>Bollea</i>			<i>Promenaea</i>		
<i>violacea</i>	+		<i>lentiginosa</i>		+
<i>Chaubardia</i>			<i>xanthina</i> 348		+
<i>heteroclita</i>	+		<i>xanthina</i> K		+
<i>klugii</i>	+		<i>Scuticaria</i>		
<i>Chaubardiella</i>			<i>hadwenii</i>	+	
<i>chasmatochila</i>	+		<i>Stenia</i>		
<i>Chondrorhyncha</i>			<i>guttata</i>	+	
<i>andreae</i>	+		<i>pallida</i>	+	
<i>andreettae</i>		+	<i>Warrea</i>		
<i>carinata</i>	+		<i>warreana</i> 508	absent	
<i>hirtzii</i>	+		<i>warreana</i> 1698	absent	
<i>lendyana</i>	+		<i>warreana</i> 1479	absent	
<i>Chondroscaphe</i>			<i>Zygopetalum</i>		
<i>escobariana</i>	+		<i>crinitum</i>	+	

<i>Cochleanthes</i>		<i>intermedium</i> K	+
<i>amazonica</i>	+	<i>mackaii</i>	+
<i>aromatica</i>	+	<i>Zygosepalum</i>	
<i>discolor</i>	+	<i>labiosum</i>	+
<i>fiabelliformis</i>	+	<i>lindeniae</i>	absent
<i>marginata</i>	+	Lycastinae	
<i>Dichaea</i>		<i>Anguloa</i>	
<i>camaridoides</i>	+	<i>clowesii</i>	absent
<i>hystricina</i>	+	<i>uniflora</i>	+
<i>chasei</i>	+	<i>virginalis</i>	absent
<i>longa</i>	+	<i>Bifrenaria</i>	
<i>muricata</i> K	+	<i>harrisoniae</i>	+
<i>trulla</i>	+	<i>inodora</i>	absent
<i>verrucosa</i>	+	<i>minuta</i>	+
<i>Galeottia</i>		<i>tyrianthina</i>	absent
<i>fimbriata</i> 1706	+	<i>Lycaste</i>	
<i>fimbriata</i> 1723	+	<i>aromatica</i>	absent
<i>negrensis</i>	+	<i>brevispatha</i>	absent
<i>grandiflora</i>	+	<i>campbellii</i>	absent
<i>Huntleya</i>		<i>ciliata</i>	absent
<i>heteroclita</i>	+	<i>consobrina</i>	absent
<i>Kefersteinia</i>		<i>dowiana</i>	absent
<i>graminea</i>	absent	<i>fulvescens</i>	absent
<i>lactea</i>	+	<i>macrobulbon</i>	absent
<i>suaveolens</i>	absent	<i>Dipteranthus</i>	
<i>Neomoorea</i>		<i>planifolius</i>	+
<i>wallisii</i>	absent	<i>Hintonella</i>	
<i>Rudolfiella</i>		<i>mexicana</i>	+
<i>floribunda</i>	absent	<i>Ornithocephalus</i>	
<i>saxicola</i>	absent	<i>bicornis</i>	+
<i>Stenocoryne</i>		<i>dolobratius</i>	+
<i>aureofulva</i>	absent	<i>gladiatus</i>	+
<i>vitellina</i>	absent	<i>inflexus</i>	+
<i>Teuscheria</i>		<i>iridifolius</i>	+
<i>dodsonii</i>	absent	<i>Phymatidium</i>	
<i>Xylobium</i>		<i>tillandsioides</i>	+
<i>colleyi</i>	absent	<i>Sphyrastylis</i>	
<i>foveatum</i>	absent	sp.	+
<i>leontoglossum</i>	+	<i>urceilabris</i>	+
<i>palmifolium</i>	absent	<i>escobariana</i>	+
<i>variegatum</i> 1757	+	<i>ecuadorensis</i>	+
<i>variegatum</i> 1066	+	<i>Zygostates</i>	
Maxillariinae		<i>alleniana</i>	+
<i>Anthosiphon</i>		Telipogoninae	
<i>roseans</i>	absent	<i>Stellilabium</i>	

<i>Cryptocentrum</i>		sp.	absent
<i>gracillimum</i>	+	<i>Telipogon</i>	
<i>Cyrtidiorchis</i>		<i>pulcher</i>	+
<i>frontinoensis</i>	+	<i>Trichoceros</i>	
Ornithocephalinae		<i>tupaipi</i>	+

Stem

Stems were available for *Aganisia*, *Batemanina*, *Dichaea*, *Galeottia*, *Neogardneria*, *Otostylis*, *Promenaea*, *Warrea*, *Zygopetalum* and *Zygosepalum*. hairs and stomata absent. cuticle smooth, from 2.5 to 3.0 μm thick in *Dichaea* to 25 μm in *Neogardneria* and 37 μm in *Zygopetalum*. epidermal cell walls heavily C- to U-thickened facing cuticle, thin-walled internally in *Aganisia*, *Galeottia*, *Neogardneria*, *Promenaea* (Fig. 10), *Zygopetalum* and *Zygosepalum*; O-thickened in *Otostylis*; thin-walled in *Dichaea* and *Warrea*. ground tissue cells thin-walled, with many variably shaped, smaller, chloroplast-containing, nucleated, assimilatory cells surrounding fewer, larger, circular to oval, empty, water-storage cells; intercellular spaces triangular, small. Inner assimilatory cells lack chloroplasts but may be rich in cruciate starch grains. vascular bundles collateral, scattered, numerous. Sclerenchyma associated with xylem and phloem poles in larger bundles, but only with phloem in smaller bundles. In all cases where both xylem and phloem sclerenchyma occur, sclerenchyma is more robust at phloem pole than at the xylem pole. fibre bundles of several sizes scattered throughout ground tissue in *Otostylis lepida* associated with stegmata containing conical silica bodies. stegmata containing conical, rough-surfaced silica bodies always occur adjacent to phloem sclerenchyma in vascular bundles. Stegmata not detected in *Promenaea xanthina*. Raphide idioblasts in unmodified cells of ground tissue.

Aerial stems in *Dichaea* differ structurally from the pseudobulbous stems characterized above. A sharply defined chlorenchymatous cortex subtends the thin-walled uniseriate epidermal layer. Endodermis and pericycle absent. ground tissue cells thin-walled, variably rounded, consisting of numerous, smaller, often chlorenchymatous, assimilatory cells some of which may contain cruciate starch grains, and fewer, larger, empty, water-storage cells. Collateral vascular bundles irregularly dispersed in the ground tissue, each encircled by sclerenchyma, more pronounced at the phloem than xylem pole, with stegmata bearing conical silica bodies adjacent to phloem sclerenchyma. In *Dichaea camaridoides* and *Dichaea chasei*, outer vascular bundles are embedded in a layer of thick-walled sclerenchyma cells, but not in *Dichaea longa*.

Root

velamen mostly 4 or 5 cells wide, up to 15 cells wide in *Warrea warreana*, cells thin-walled, somewhat thickened in *Ackermania caudata*, *Galeottia negrensis* and *Scuticaria hadwenii*; epivelamen cells may be isodiametric, periclinal or even both

in the same specimen; endovelamen cells polygonal isodiametric, anticlinal, or outer cells isodiametric and inner cells anticlinal; cell walls with tenuous spiral thickenings (Fig. 5), these somewhat thickened in *Scuticaria* , occasionally running at divergent angles, walls sometimes with wide openings. tilosomes absent. exodermal cells polygonal, anticlinal, quadrangular, or periclinal (*Dichaea*), thin-walled, or with slightly thickened outer and lateral walls; passage cells intermittent, nucleated, frequently with thickened outer walls; lateral walls of long cells with ladder-like thickenings (Fig. 5). cortex 5 (*Dichaea*) to 19 cells wide (*Ackermania caudata*); cells thin-walled, oval but mostly circular, except for thicker-walled, angular idioblasts with birefringent cell walls; cell walls have branched, banded thickenings in *Chaubardia heteroclita* , *Koellensteinia graminea* and *Neogardneria murrayana*. Intercellular spaces triangular. Chloroplasts and cruciate starch grains occupy cortical cells of some species. Cells often infested with hyphae, sometimes forming pelotons, and dead fungal masses common. Raphides in unmodified cells. endodermis uniseriate; cells basically isodiametric, tending toward periclinal in *Cochleanthes aromatica* , *Koellensteinia* sp., *Neogardneria murrayana* , *Pabstia viridis* and *Zygopetalum mackaii* ; mostly periclinal in *Paradisianthus micranthus*. Cells U-thickened opposite phloem (Fig. 11), very heavily so in *Ackermania caudata* and *Ackermania cornuta* , *Chondroscaphe escobariana* , *Dichaea muricata* and *Scuticaria hadwenii* ; O-thickened in *Bollea violacea* ; thin-walled in *Paradisianthus micranthus*. pericycle cells isodiametric, O-thickened opposite phloem; thin-walled in *Paradisianthus micranthus* . vascular cylinder 6-arch (*Dichaea muricata* , *Paradisianthus micranthus* , *Zygosepalum lindeniae*), 9-arch in *Promenaea xanthina* (Fig. 11) and up to 18-arch (*Otostylis lepida*), xylem in radial rows alternating with circular, oval and elliptical clusters of phloem cells. Vascular tissues embedded in thick-walled sclerenchyma cells (Fig. 11); thin-walled in *Paradisianthus micranthus* and *Pescatoria cerina*. pith cells circular, thin-walled, parenchymatous; thick-walled in *Ackermania caudata* , *Batemanianthus colleyi* , *Dichaea muricata* , *Promenaea lentiginosa* and *Scuticaria hadwenii*. Intercellular spaces triangular. Raphides in unmodified cortical cells.

Lycastinae

Leaf

Surface. hairs glandular, ad- and abaxial (Fig. 12), obpyriform, sunken, single-celled, arising from a basal cell, apex thick-walled, not exserted. stomata abaxial, tetracytic. Epidermal cells polygonal, isodiametric, abaxial often elongated parallel to veins, walls straight-sided and curvilinear.

Section. cuticle smooth, wavy in *Stenocoryne* , 2.5 μm both surfaces to 12.5 μm thick adaxially, 7.5 μm abaxially in *Rudolfiella* . epidermal cells mostly isodiametric both surfaces, sharply periclinal adaxially in *Stenocoryne* ; outer walls thickest. stomata superficial, sunken in *Rudolfiella* and *Stenocoryne* , substomatal chambers small, outer ledges small, moderate in *Rudolfiella* and *Stenocoryne* , ruminant and enhanced by extended cuticular 'horns' in *Bifrenaria harrisoniae* ; inner ledges

obscure to apiculate. hypodermis absent. fibre bundles in a single row alternating between vascular bundles in *Anguloa virginalis* and *Bifrenaria harrisoniae* and abaxially between vascular bundles in *Stenocoryne aureofulva* and *Rudolfiella floribunda* ; ad- and abaxial rows in *Teuscheria dodsonii* and *Xylobium*. mesophyll homogeneous, cells oval, circular and irregular, crowded, thin-walled, somewhat thick-walled in *Bifrenaria harrisoniae* and *Teuscheria dodsonii* ; heterogeneous in *Bifrenaria minuta* , *Rudolfiella floribunda* , *Rudolfiella saxicola* and *Stenocoryne aureofulva* (homogeneous in *Stenocoryne vitellina*) . Palisade mesophyll cells in *Bifrenaria harrisoniae* and *Bifrenaria minuta* 2–4 cells wide, 2 cells in *Rudolfiella floribunda* and *Rudolfiella saxicola* , 1 cell in *Stenocoryne aureofulva* ; cells thin-walled, somewhat thick-walled in *Bifrenaria harrisoniae* . Intercellular spaces triangular. Raphide idioblasts thin-walled, circular in T-S, saccate in L-S. vascular bundles collateral in one row. Midvein and larger bundles in *Anguloa virginalis* and *Teuscheria dodsonii* with a central abaxial vascular bundle flanked on either side adaxially by a supernumerary vascular bundle. In *Teuscheria dodsonii* the larger bundles are often elliptical with the long axis paralleling the epidermises. Sclerenchyma ‘caps’ present at both poles, except in *Bifrenaria harrisoniae* , and absent in the smallest bundles; sclerenchyma is always stronger at the phloem than at the xylem pole. Stegmata bearing conical rough-surfaced silica bodies accompany vascular bundle sclerenchyma and fibre bundles. Bundle sheaths more or less continuous in *Anguloa virginalis* , *Bifrenaria harrisoniae* and *Stenocoryne aureofulva* ; ill-defined in *Lycaste deppei* and *Teuscheria dodsonii* ; more or less complete around smaller bundles in *Xylobium* , ill-defined around larger bundles; all cells thin-walled and chlorophyllous.

Stem

hairs and stomata absent. cuticle ranges from 10.0 µm in *Xylobium variegatum* to 37.5 µm in *Rudolfiella floribunda* ; wavy in *Anguloa virginalis* , smooth in other taxa. epidermal cells isodiametric in *Anguloa virginalis* , *Rudolfiella floribunda* and *Xylobium variegatum* , elliptical in *Bifrenaria harrisoniae* , *Lycaste ciliata* , *Neomoorea wallisii* and *Stenocoryne aureofulva* . Cell walls thick, evenly distributed in *Anguloa virginalis* , thin-walled adjacent to internal tissues in other taxa. cortex and endodermis absent in *Anguloa virginalis* , *Bifrenaria harrisoniae* , *Rudolfiella floribunda* , *Stenocoryne aureofulva* and *Xylobium variegatum* ; cortex a 1- or 2-cell layer of thick-walled cells in *Lycaste ciliata* and *Neomoorea wallisii* lacking an endodermis. ground tissue with larger circular and oval, thin-walled, empty water-storage cells surrounded by smaller, circular, oval and variably shaped assimilatory cells that may bear cruciate starch grains and chloroplasts in outer layers of *Stenocoryne aureofulva* and *Xylobium variegatum* . vascular bundles collateral, numerous, scattered; in *Neomoorea wallisii* small bundles are peripheral. Sclerenchyma present at both poles in larger bundles, only at phloem pole in smaller bundles; in *Bifrenaria harrisoniae* , sclerenchyma present only at phloem pole in all bundles. Scattered fibre bundles in *Bifrenaria harrisoniae* and *Xylobium variegatum* ; they form an ill-defined row inside the cortex of *Lycaste ciliata* and are peripheral in *Neomoorea wallisii* . Stegmata with conical, rough-surfaced silica bodies occur

next to phloem and xylem sclerenchyma in larger bundles, but only at phloem sclerenchyma in *Bifrenaria harrisoniae*, *Rudolphiella floribunda* and *Stenocoryne aureofulva*. Stegmata occur along fibre bundles. Raphides in unmodified cells.

Root

velamen 3 cells wide in *Teuscheria dodsonii*, up to 11 cells wide in *Lycaste deppei*. Epivelamen cells isodiametric, periclinal in *Neomoorea wallisii*; endovelamen cells isodiametric externally, tending to anticlinal internally in *Anguloa ruckeri*, *Lycaste deppei*, *Neomoorea wallisii*, *Stenocoryne aureofulva* and *Xylobium leontoglossum*; anticlinal throughout in *Bifrenaria harrisoniae* and *Rudolphiella saxicola*; isodiametric in *Teuscheria dodsonii*. Cell walls thin, somewhat thickened in *Teuscheria dodsonii*. Fine spiral thickenings present. Root hairs unicellular. tilosomes present in *Anguloa ruckeri* (Fig. 4), *Lycaste deppei*, *Neomoorea wallisii* and *Xylobium leontoglossum*; absent in *Bifrenaria harrisoniae*, *Rudolphiella saxicola*, *Stenocoryne aureofulva* and *Teuscheria dodsonii*. exodermis cells square with anticlinal tendency in *Anguloa ruckeri*, square in other taxa; somewhat thick-walled throughout in *Anguloa ruckeri*, *Lycaste deppei* and *Xylobium leontoglossum*; thin-walled in other taxa. Lateral walls of long cells with ladder-like thickenings. Passage cells intermittent. Nuclei frequently present in 'dead' cells. cortex up to 9 cells wide; cells thin-walled, more or less circular and oval; branched bands of secondary cell wall material occur in *Rudolphiella saxicola*, *Stenocoryne aureofulva* (but not in *Stenocoryne vitellina*) and *Xylobium leontoglossum*. Branched bands occur in *Bifrenaria wendlandiana* but not in *Bifrenaria harrisoniae*. Angular, empty idioblasts with thickened birefringent cell walls occur in all taxa. Triangular intercellular spaces occur among cortical cells. Pelotons and dead hyphal masses common. endodermis cells isodiametric, O-thickened adjacent to phloem; periclinal, thin-walled in *Neomoorea wallisii*, U-thickened opposite phloem in *Teuscheria dodsonii*. pericycle cells isodiametric, O-thickened opposite phloem. stegmata with conical, rough-surfaced silica bodies replace pericycle cells opposite phloem in *Anguloa ruckeri* (Fig. 13), *Anguloa uniflora*, *Bifrenaria harrisoniae* (stegmata also occur in *Bifrenaria tetragona* and *Bifrenaria wendlandiana*, but not in *Bifrenaria tyrianthina*), *Lycaste deppei*, *Lycaste suaveolens*, *Lycaste macrobulbon*, *Neomoorea wallisii*, *Stenocoryne aureofulva*, *Stenocoryne vitellina*, *Xylobium leontoglossum*, *Xylobium colleyi*, *Xylobium foveatum*, *Xylobium palmifolium* and *Xylobium variegatum*; absent in *Rudolphiella saxicola*, *Rudolphiella floribunda* and *Teuscheria dodsonii*. The base of the silica body faces the phloem, the tip the endodermis. vascular cylinder 8- to 19-arch. Xylem rays alternate with elliptical and circular clusters of phloem cells. Vascular tissues embedded in somewhat thin-walled sclerenchyma; in *Bifrenaria harrisoniae* thin-walled, circular sclerenchyma cells merge centripetally with thicker-walled, angular parenchyma cells. pith cells circular, thin-walled with triangular intercellular spaces; in *Rudolphiella saxicola* pith cells angular and thick-walled, in *Rudolphiella floribunda* circular and thin-walled; in *Teuscheria dodsonii*, pith cells angular and thick-walled.

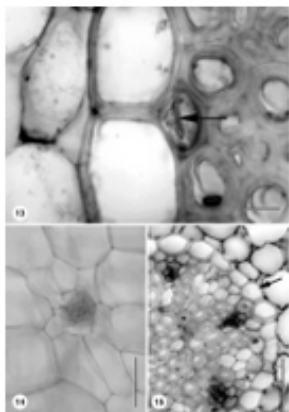


Figure 13–15. Fig. 13. *Anguloa ruckeri*. T-S root showing stegma containing a conical silica body (arrow). Stegmata replace pericycle cells in roots of some orchid species. Scale bar = 10 μm . Fig. 14. *Cyrtidiorchis frontinoensis*. Leaf scraping showing glandular hair in face view. Scale bar = 50 μm . Fig. 15. *Ornithocephalus inflexus*. T-S root to illustrate O-thickened endodermal cell walls (arrow) opposite phloem and thick-walled pith cells. Scale bar = 50 μm .

Maxillariinae

Leaf

Surface. hairs ad- and abaxial, sunken, glandular (Fig. 14), one-celled arising from a basal cell, not exerted. stomata abaxial, on both surfaces in *Cryptocentrum gracillimum* ; tetracytic; epidermal cells rectangular, elongated parallel with veins in *Anthosiphon roseans* and *Cryptocentrum gracillimum* ; polygonal, isodiametric with straight and curvilinear walls in *Cyrtidiorchis frontinoensis* .

Section. cuticle 2.5 μm thick, both surfaces in *Anthosiphon roseans* and *Cryptocentrum gracillimum* , adaxial to 5.0 μm in *Cyrtidiorchis frontinoensis* , abaxial 2.5 μm epidermal cells isodiametric in *Anthosiphon roseans* and *Cryptocentrum gracillimum* , periclinal in *Cyrtidiorchis frontinoensis* , outer walls thickest. stomata superficial, substomatal chamber small; outer ledges moderate in *Anthosiphon roseans* , ruminant in *Cyrtidiorchis frontinoensis* , deteriorated in *Cryptocentrum gracillimum* ; inner ledges obscure, apiculate. hypodermis absent in *Anthosiphon roseans* and *Cyrtidiorchis frontinoensis* , present in *Cryptocentrum gracillimum* as a row of few-celled fibre bundles interrupted by chlorenchyma cells, abutting the epidermis and surrounding the leaf; fibres not associated with stegmata. Ad- and abaxial rows of fibre bundles in *Anthosiphon roseans* , absent in *Cyrtidiorchis frontinoensis* . mesophyll homogeneous, 4 or 5 cells wide in *Anthosiphon roseans* ; 12–14 cells wide in *Cyrtidiorchis frontinoensis* , upper two-thirds occupied by large, circular, thin-walled, chloroplast-free, nucleated apparent water-storage cells, lower one-third with very small, circular and oval, thin-walled, chloroplast-containing cells; leaf isobilateral in *Cryptocentrum gracillimum* , palisade cells developed toward both surfaces separated by a row of vascular bundles, shorter cells separate palisade tissues from epidermal layers; 1 or 2 layers of more or less circular, thin-walled cells extend between vascular bundles in the centre of the leaf. Intercellular spaces small, triangular. Crystalliferous idioblasts circular in T-S, saccate, blunt-ended in L-S. vascular bundles collateral, in one series. Sclerenchyma at both poles, except in *Cryptocentrum gracillimum* where it is always present at the phloem pole but lacks at the xylem pole in smaller bundles. stegmata

with conical, rough-surfaced silica bodies present adjacent to vascular bundle sclerenchyma and fibre bundles, except absent in *Cyrtidiorchis frontinoensis*. Bundle sheath absent in *Anthosiphon roseans*; mostly obscure, incomplete in *Cryptocentrum gracillimum*, complete in *Cyrtidiorchis frontinoensis*; cells thin-walled, chlorenchymatous. In a large vein of one specimen there is an abaxial centrally located vascular bundle flanked by two adaxial supernumerary bundles; in another specimen, large veins have as many as six supernumerary bundles in three pairs.

Root

Roots unavailable for *Anthosiphon roseans*. velamen 2–4 cells wide, epivelamen cells more or less isodiametric; outer endovelamen cells isodiametric in *Cryptocentrum gracilipes* and *Neomoorea wallisii*, anticlinal internally, sharply anticlinal throughout in *Cyrtidiorchis frontinoensis*. Cell walls somewhat thickened in *Cryptocentrum gracilipes* and *Cyrtidiorchis frontinoensis*. Spiral thickenings coarse, anticlinally parallel in *Cyrtidiorchis frontinoensis*, deteriorated in *Cryptocentrum frontinoensis*. Hyphae widespread in *Cryptocentrum frontinoensis*. tilosomes present, lamellate in *Cyrtidiorchis frontinoensis*. exodermis cells more or less isodiametric in *Cryptocentrum gracilipes*, squarish in *Cyrtidiorchis frontinoensis* with ladder-like thickenings in lateral walls of long cells, U-thickened in *Cryptocentrum gracilipes*, and heavily O-thickened in *Cyrtidiorchis frontinoensis*. cortex 5–7 cells wide, cells circular to oval, walls more or less thickened in *Cryptocentrum gracilipes* and *Cyrtidiorchis frontinoensis*. Angular, thick-walled idioblasts absent in *Cryptocentrum gracilipes* and *Cyrtidiorchis frontinoensis*. Masses of dead hyphae present. endodermis cells isodiametric in *Cryptocentrum gracilipes* and *Cyrtidiorchis frontinoensis*; O-thickened opposite phloem in *Cryptocentrum gracilipes*, U-thickened in *Cyrtidiorchis frontinoensis*. pericycle cells somewhat periclinal in *Cryptocentrum gracilipes*, isodiametric in *Cyrtidiorchis frontinoensis*; O-thickened opposite phloem in *Cryptocentrum gracilipes*, and *Cyrtidiorchis frontinoensis*. vascular cylinder 6-arch in *Cryptocentrum gracilipes*, 20-arch in *Cyrtidiorchis frontinoensis*. Radial rows of xylem cells alternate with oval and elliptical clusters of phloem cells. Vascular tissue embedded in sclerenchyma. Pith cells sclerified in *Cryptocentrum gracilipes*, but thin-walled, parenchymatous in *Cyrtidiorchis frontinoensis*. Intercellular spaces lacking in *Cryptocentrum gracilipes*, triangular in *Cyrtidiorchis frontinoensis*.

Ornithocephalinae

Leaf

All genera in this group have thickened, small leaves, sometimes laterally flattened along the mid-vein so that only the abaxial surface is exposed; other times leaves are subterete. Adaxial cells occur where there is a foliar groove.

Surface. hairs absent. stomata abaxial, basically tetracytic but with significant permutations giving rise, for example, to cyclocytic, anomocytic and anisocytic configurations in different taxa with varying numbers of subsidiary cells. Epidermal cells rectangularly elongate in *Hintonella mexicana* and *Sphyrastylis ecuadorensis* **to polygonal with straight and curvilinear walls in *Ornithocephalus gladiatus*.**

Section. cuticle 2.5 μm but 5.0–12.5 μm in *Dipteranthus planifolius*, smooth. epidermal cells isodiametric, papillate in *Dipteranthus planifolius*; isodiametric and periclinal adaxially, periclinal abaxially in *Hintonella mexicana*; isodiametric in the adaxial groove and on the abaxial surface in *Ornithocephalus inflexus*; isodiametric both surfaces of *Phymatidium tillandsioides*; more or less periclinal both surfaces of *Sphyrastylis ecuadorensis*; and isodiametric both surfaces of *Zygostates alleniana*. stomata superficial in *Dipteranthus planifolius* and *Zygostates alleniana*, slightly raised in *Hintonella mexicana*, *Ornithocephalus inflexus*, *Phymatidium tillandsioides* and *Sphyrastylis ecuadorensis*. Substomatal chambers small, moderate in *Phymatidium tillandsioides*; outer ledges obscure in *Dipteranthus planifolius*, *Hintonella mexicana* and *Ornithocephalus inflexus*, moderate to pronounced in *Phymatidium tillandsioides*, *Sphyrastylis ecuadorensis* and *Zygostates alleniana*; inner ledges obscure throughout. hypodermis and fibre bundles absent. mesophyll homogeneous, varying in thickness according to the configuration of the leaf. Cells all thin-walled, organization highly variable: *Dipteranthus planifolius* – larger cells empty, cell walls provided with branching, birefringent bands of secondary wall material; smaller cells crowded, chlorophyllous, circular and elliptical; *Hintonella mexicana* – tendency toward isobilateralism, larger, empty cells have branched bands of secondary wall material, smaller cells crowded, chlorophyllous, variably shaped, circular to oval; *Ornithocephalus inflexus* – larger cells empty with spirally arranged slender bands of birefringent secondary wall material; smaller cells with cruciate starch grains; *Phymatidium tillandsioides* – larger, central, thin-walled empty cells surrounded peripherally by smaller, almost circular chlorophyllous cells; *Sphyrastylis ecuadorensis* – larger, oval, empty cells with reticulate, wide-meshed wall thickenings and smaller, oval, thin-walled chlorophyllous cells also containing cruciate starch grains; *Zygostates alleniana* – larger, oval, empty cells with conspicuous spiral wall thickenings and smaller, oval and circular chlorophyllous cells. In all cases above, the larger cells serve for water storage. vascular bundles collateral, variously arranged in accordance with the overall configuration of the leaf: *Dipteranthus planifolius* has four bundles on either side of the central bundle; *Hintonella mexicana* has a central bundle flanked by two on either side; *Ornithocephalus inflexus* has two or three bundles in a linear series followed by several sets of paired bundles; *Phymatidium tillandsioides* has only three vascular bundles; *Sphyrastylis ecaudorensis* has a linear series of bundles in which the phloem faces the tip margin of the leaf, and paired bundles in which the phloem faces the abaxial epidermis; *Zygostates alleniana* has four bundles on each side of the central largest bundle. Sclerenchyma always accompanies phloem, though in *Dipteranthus planifolius*, *Hintonella mexicana* and *Zygostates alleniana* it is represented only by a few, thin-walled cells. Sclerenchyma is absent at the xylem

pole in *Dipteranthus planifolius* and *Hintonella mexicana*, and only present there in the larger bundles of *Ornithocephalus inflexus*, *Phymatidium tillandsioides*, *Sphyrastylis ecuadorensis* and *Zygostates alleniana*. stegmata absent in *Dipteranthus planifolius*, *Hintonella mexicana*, *Ornithocephalus inflexus*, *Sphyrastylis ecuadorensis* and *Zygostates alleniana*; they occur only in *Phymatidium tillandsioides* associated with phloem sclerenchyma. Bundle sheaths mostly indistinct, except sometimes well defined in *Ornithocephalus inflexus*; cells thin-walled with chloroplasts, except in *Dipteranthus planifolius*. Raphides in thin-walled idioblasts, circular in T-S.

Stem

Stems were available only for *Dipteranthus planifolius* and *Phymatidium tillandsioides*. hairs and stomata absent. cuticle 10.0–17.5 µm thick in *Dipteranthus planifolius*, smooth and less than 2.5 µm in *Phymatidium tillandsioides*, smooth. epidermal cells periclinal and isodiametric, outer wall much thickened in *Dipteranthus planifolius*, very thin in *Phymatidium tillandsioides*. cortex absent in *Dipteranthus planifolius*; in *Phymatidium tillandsioides* there are one to three layers of thick-walled cells resembling an exodermis immediately subjacent to the epidermis followed internally by a two- or four-layered region of oval, somewhat compressed, thin-walled cells with triangular intercellular spaces; endodermis and pericycle absent. ground tissue. Fewer, larger, empty, somewhat collapsed cells surrounded by many smaller, assimilatory cells with cruciate starch grains and chloroplasts in outer layers in *Dipteranthus planifolius*. Parenchymatous tissue of outer layers is confluent with the pith between the vascular bundles. In *Phymatidium tillandsioides* assimilatory cells oval, contain cruciate starch grains; intercellular spaces triangular. vascular bundles collateral, forming a ring of 11 bundles in *Dipteranthus planifolius*; a ring of peripheral bundles with many bundles scattered in the ground tissue occur in *Phymatidium tillandsioides*. Sclerenchyma occurs at both poles in larger bundles in *Dipteranthus planifolius*, absent at xylem pole in smaller bundles; present at both poles in *Phymatidium tillandsioides*. stegmata absent, both species.

Root

velamen two or three cells wide, four or five in *Sphyrastylis ecuadorensis*. Epivelamen cells isodiametric; endovelamen cells various, outer cells isodiametric, inner cells anticlinal; cell walls thickish; spiral thickenings coarse. Cell walls with elliptical pits in *Dipteranthus planifolius* and *Sphyrastylis ecuadorensis*. tilosomes absent. exodermis cells squarish, sometimes anticlinal, evenly thin-walled, ladder-like thickenings on lateral walls of long cells; passage cells intermittent, inflated in *Sphyrastylis ecuadorensis*. cortex four to six cells wide, eight or nine in *Sphyrastylis ecuadorensis*. Cells thin-walled, circular and oval. Angular idioblasts with birefringent cell walls occur in *Dipteranthus planifolius*, *Hintonella mexicana* and *Sphyrastylis ecuadorensis*; absent in *Ornithocephalus inflexus*, *Phymatidium tillandsioides* and *Zygostates alleniana*. Larger, possibly water-storage, cells in

Hintonella mexicana have branched, secondary cell wall thickenings. Cruciate starch grains occur in *Sphyrastylis ecuadorensis*. Cells in *Ornithocephalus inflexus* infested with hyphal pelotons and masses of dead hyphae. endodermis cells isodiametric, 0-thickened opposite phloem (Fig. 15), very thick-walled in *Dipteranthus planifolius*, *Phymatidium tillandsioides* and *Sphyrastylis ecuadorensis*. pericycle as endodermis. vascular cylinder four- or five-arch, 10-arch in *S. ecuadorensis*, xylem in radial rows, except clusters in *Ornithocephalus inflexus* and *Zygostates alleniana*, alternating with circular and elliptical clusters of phloem cells. Vascular tissue embedded in sclerenchyma. pith sclerotic with angular cells, intercellular spaces absent.

Telipogoninae

Leaf

Surface. hairs sunken, both surfaces in *Stellilabium*, none in *Telipogon pulcher* and *Trichoceros tupaipi*. stomata abaxial only, tetracytic; epidermis deteriorated in *Stellilabium*, cells polygonal in *Telipogon pulcher* and *Trichoceros tupaipi*, walls straight and curvilinear.

Section. cuticle less than 2.5 μm thick both surfaces in *Stellilabium* and *Telipogon pulcher*, smooth; up to 5.0 μm in *Trichoceros tupaipi*, vaulted, smooth. epidermal cells irregularly isodiametric both surfaces in *Stellilabium* and *Telipogon pulcher* and upper epidermis in *Trichoceros tupaipi*, but lower epidermis periclinal in *Trichoceros tupaipi*. stomata superficial. Substomatal chambers small, outer ledges moderate in *Telipogon pulcher*, obscure in *Trichoceros tupaipi*; inner ledges obscure, apiculate. hypodermis absent. fibre bundles absent. mesophyll homogeneous in *Stellilabium* and *Telipogon pulcher*. Deterioration prevents enumerating cell thickness in *Stellilabium*; adaxial two-thirds thickness consists of thin-walled larger mainly empty cells, a few of which have chloroplasts and serve for water-storage; cells of the lower one-third are circular and oval, and rich in chloroplasts. Mesophyll in *Telipogon pulcher* is 5 cells wide, cells are thin-walled, circular and oval, crowded with small triangular intercellular spaces. Mesophyll in *Trichoceros tupaipi* is heterogeneous; adaxial palisade layer is 2 or 3 cells wide, abaxial layer is 7–9 cells wide. All cells chlorophyllous, thin-walled, circular and oval, except upright cells in *Trichoceros tupaipi* that occupy more than one-half leaf transection. Ad- and abaxial cell layers are roughly divided by the row of vascular bundles. Enormous thin-walled crystalliferous idioblasts, measuring up to 182 μm in transectional diameter, occur in the mesophyll of *Stellilabium* occupying large portions of the leaf (Fig. 16). vascular bundles collateral in one series. In *Stellilabium* there are only 3 vascular bundles. There is no sclerenchyma associated with the vascular bundles in *Stellilabium* (Fig. 17); sclerenchyma occurs at both xylem and phloem poles in *Telipogon pulcher* and *Trichoceros tupaipi*, although in the latter it is absent at the xylem pole in the smallest bundles. Stegmata with conical, rough-surfaced silica bodies appear associated with sclerenchyma in these two species. Bundle sheaths are usually indistinct and incomplete, but some

complete sheaths occur in *Trichoceros tupaipi*. Bundle sheath cells thin-walled and chloroplast-containing.

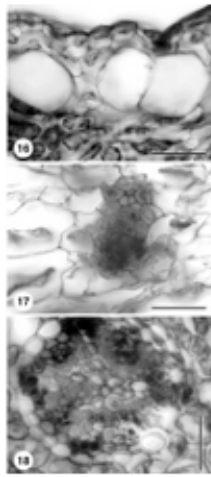


Figure 16–18. Fig. 16. *Stellilabium* sp. T-S leaf with greatly enlarged raphide idioblasts. Scale bar = 100 μ m. Fig. 17. *Stellilabium* sp. T-S leaf showing vascular bundle unaccompanied by sclerenchyma. Scale bar = 50 μ m. Fig. 18. *Stellilabium* sp. T-S root with thick-walled pith cells. Scale bar = 50 μ m.

Stem

Stems were available only for *Telipogon pulcher*. hairs and stomata absent. cuticle 5.0–7.5 μ m thick, smooth. epidermal cells more or less periclinal, thin-walled. cortex 2-layered. Outer layer abutting epidermis about 5 cells wide, cells mostly oval, thin-walled, lacking chloroplasts, larger than cells of inner layer. Inner layer 3 cells wide, distinctly oval, thin-walled, lacking chloroplasts. Large water-storage cells occur in portions of the cortex. endodermis and pericycle lacking. ground tissue cells round, parenchymatous, thick-walled with conspicuous triangular intercellular spaces. Outer layer of vascular cylinder 3–5 cells wide, cells thick-walled. vascular bundles collateral, many; peripheral bundle ring surrounding inner scattered bundles invested in thick-walled cells. Phloem sclerenchyma cells thick-walled, laminated; xylem sclerenchyma absent. stegmata absent.

Root

velamen one- or two-layered in *Stellilabium*, three- or four-layered in *Telipogon pulcher*, sloughed off in *Trichoceros antennifer*. Epivelamen cells in *Stellilabium* periclinal, isodiametric in *Telipogon pulcher*; endovelamen cells in *Stellilabium* periclinal and isodiametric, isodiametric in *Telipogon pulcher*. Cell walls thickened with fine spiral thickenings in *Stellilabium*, absent (?) in *Telipogon pulcher*. Hyphae present in *Telipogon pulcher*. tilosomes absent. exodermis cells thin-walled, somewhat externally thickened in *Telipogon pulcher*, polygonal, squarish in *Stellilabium*; anticlinal in *Telipogon pulcher* and *Trichoceros antennifer*, outer walls vaulted in *Telipogon pulcher*. Passage cells intermittent. cortex cells thin-walled, circular to oval, with triangular intercellular spaces. Cortex to 13 cell layers wide in *Telipogon pulcher*. Many cells with birefringent walls and angular outlines. Cells in *Telipogon pulcher* have branched, banded, secondary cell wall thickenings.

Dead hyphal masses occur as well as pelotons. endodermis cells isodiametric and periclinal in *Telipogon pulcher*, 0-thickened walls opposite phloem stratified. pericycle as endodermis. vascular cylinder 5-arch in *Stellilabium*, 13-arch in *Telipogon pulcher*, and 10-arch in *Trichoceros antennifer*; xylem in radial rows alternating with circular clusters of phloem cells. Vascular tissue embedded in sclerenchyma. Pith cells sclerotic in *Stellilabium* (Fig. 18), cells polygonal; walls very thick; cells thin-walled, circular in *Telipogon pulcher* and *Trichoceros antennifer*; intercellular spaces triangular.

RESULTS AND DISCUSSION

Anatomy

Stegmata are conical cells that contain silica deposits. These cells, at least in orchids, are always associated intimately with fibres in leaves and stems and have recently been shown to occur in pericycle cells of roots in certain species. As noted by Møller & Rasmussen (1984), Mettenius (1864) was probably the first to recognize stegmata (in the cortex of the petiole and stem and in the veins of the leaf tip) as individual cells containing silica, or 'Concretionen von Kieselsäure' in the filmy ferns, Hymenophyllaceae, tree ferns, Cyatheaceae, other ferns, and monocots. Solereder & Meyer (1930) published a review of the presence, shape of silica bodies and position in the plant of stegmata based on the work of 14 authors and their own observations. The main forms of silica bodies were globular and conical. They reported the presence of silica bodies in the axis, rhizome, pseudobulb, leaf and floral axis. There is no mention of stegmata in roots. Møller & Rasmussen (1984) recorded observations on 132 orchid specimens in which they noted the presence, form and site of stegmata. They concluded that root tissues did not have stegmata, even if they occurred in other plant parts. Holtzmeier et al. (1998) pointed to the presence of stegmata with conical silica bodies in pericycle cells adjacent to phloem clusters in roots of *Maxillaria picta*, and noted their occurrence in species of *Xylobium* and *Neomoorea wallisii* (Lycastinae). Subsequently, Yukawa & Stern, (2002) reported stegmata in roots of some species of *Cymbidium*, and Stern & Judd (2002) expanded the distribution of stegmata in roots of additional taxa.

Table 6 contains a comparison of selected anatomical features among taxa of Maxillarieae. Stegmata characterize leaves of Cryptarrheninae, Zygopetalinae, Lycastinae and Maxillariinae. Within the Maxillariinae subtribe, they are absent only in *Cyrtidiorchis*. In *Ornithocephalinae*, stegmata appear solely in leaves of *Phymatidium*. They are lacking in leaves of *Stellilabium* but are present in *Telipogon* and *Trichoceros*. Stegmata with conical silica bodies are present along the fibre bundles and vascular sclerenchyma in leaves of *Maxillaria*, *Mormolyca* and *Trigonidium* (Holtzmeier et al., 1998).

Table 6. Comparison of selected anatomical features of Maxillarieae

	Stegmata ⁺						
Taxon	Leaf	Stem	Root	Tilosomes	Foliar glands	Foliar fibre bundles	Endodermal cell wall thickenings
Cryptarrheninae							
<i>Cryptarrhena</i>							
<i>guatemalensis</i>	+	+	–	–	–	–	
<i>lunata</i>	+			–	–	–	thin
Zygopetalinae							
<i>Ackermania</i>							
<i>caudata</i>	+		–	–	–	–	U
<i>cornuta</i>	+		–	–	–	–	U
<i>Aganisia</i>							
<i>cyanea</i>	+	+	–	–	–	–	U
<i>Batemania</i>							
<i>ciliata</i>	+	+		–	–	–	U
<i>Bollea</i>							
<i>violacea</i>	+		–	–	–	–	O
<i>Chaubardia</i>							
<i>klugii</i>	+		–	–	–	–	U
<i>Chaubardiella</i>							
<i>dalessandroi</i>	+		–	–	–	–	U
<i>Chondrorhyncha</i>							
<i>lendyana</i>	+		–	–	–	–	U
<i>Chondroscaphe</i>							
<i>escobariana</i>	+		–	–	–	–	U
<i>Cochleanthes</i>							
<i>aromatica</i>	+		–	–	–	–	U
<i>Dichaea</i>							
<i>muricata</i>	+		–	–	–	–	U
<i>Galeottia</i>							
<i>fimbriata</i>	+		–	–	–	–	U
<i>Huntleya</i>							
<i>heteroclita</i>	+		–	–	–	–	U
<i>Kefersteinia</i>							
sp. 1749	+		–	–	–	–	U
<i>Koellensteinia</i>							
<i>altissima</i>	+		–	–	–	+	O
<i>Neogardneria</i>							
<i>murryana</i>	+		–	–	–	–	U
<i>Otostylis</i>							
<i>lepida</i>	+	+	–	–	–	+	U
<i>Pabstia</i>							
<i>viridis</i>	+		–	–	–	–	U
<i>Paradisianthus</i>							
<i>micranthus</i>			–	–			thin

<i>Pescatoria</i>							
<i>cerina</i>	+		–	–	–	–	U
<i>Promenaea</i>							
<i>lentiginosa</i>	+	+	–	–	–	–	U
<i>xanthina</i>		–	–	–	–	–	U
<i>Scuticaria</i>							
<i>hadwenii</i>	+		–	–	–	+	U
<i>Stenia</i>							
<i>pallida</i>	+		–	–	–	–	U
<i>Warrea</i>							
<i>warreana</i>	+	+	–	–	–	–	O
<i>Zygopetalum</i>							
<i>mackail</i>	+	+	–	–	–	– [†]	U
<i>Zygosepalum</i>							
<i>lindeniae</i>	+	+	–	–	–	–	U
<i>Lycastinae</i>							
<i>Anguloa</i>							
<i>virginalis</i>	+	+			+	+	
<i>ruckeri</i>			+	+			O
<i>Bifrenaria</i>							
<i>harrisoniae</i>	+	+	+	+	+	+	O
<i>Lycaste</i>							
<i>deppoi</i>	+			+	+	+	O
<i>ciliata</i>		+	+				
<i>Neomoorea</i>							
<i>wallisii</i>	+	+	+	+	+	+	thin
<i>Rudolfiella</i>							
<i>floribunda</i>	+	+	–	–	+	+	thin
<i>saxicola</i>			–	–	+	+	O
<i>Stenocoryne</i>							
<i>aureofulva</i>	+	+	+	–	+	+	O
<i>Teuscheria</i>							
<i>dodsonii</i>	+		–	–	+	+	U
<i>Xylobium</i>							
<i>variegatum</i>	+	+	+	+	+	+	O
<i>Maxillariinae</i>							
<i>Anthosiphon</i>							
<i>roseans</i>	+				+	+	
<i>Cryptocentrum</i>							
<i>gracillimum</i>	+				+	+	O
<i>gracilipes</i>			–	+			
<i>Cyrtidiorchis</i>							
<i>frontinoensis</i>	–		–	+	+	–	U
<i>Ornithocephalinae</i>							
<i>Dipteranthus</i>							
<i>planifolius</i>	–	–	–	–	–	–	O

<i>Hintonella</i>							
<i>mexicana</i>	-		-	-	-	-	o
<i>Ornithocephalus</i>							
<i>inflexus</i>	-		-	-	-	-	o
<i>Phymatidium</i>							
<i>tillandsioides</i>	+	-	-	-	-	-	o
<i>Sphyrastylis</i>							
<i>ecuadorensis</i>	-		-	-	-	-	o
<i>Zygostates</i>							
<i>alleniana</i>	-		-	-	-	-	o
<i>Telipogoninae</i>							
<i>Stellilabium</i>							
sp.	-		-	-		-	
<i>Telipogon</i>							
<i>pulcher</i>	+	-	-	-	-	-	o
<i>Trichoceros</i>							
<i>antennifer</i>			-	-	-	-	o
<i>tupaipi</i>	+						

* Blank spaces indicate a lack of material.

† Foliar fibre bundles present in *Z. crinitum* and *Z. intermedium*.

Stems of *Cryptarrhena guatemalensis* have stegmata. In Zygotetralinae, where stems were available for study, they occur in all species, except *Promenaea xanthina*, although they appear in *P. lentiginosa*. They are absent in available stems of *Ornithocephalinae* and *Telipogoninae*.

Stegmata in roots occur in all material of Lycastinae, except for the two species of *Rudolfiella*. They are absent in roots of all other *Maxillarieae* investigated.

It is noteworthy that no function has been ascribed to stegmata containing silica bodies. However, Holtzmeier et al. (1998) thought these structures, aligned along the margins of fibres, might provide additional structural support, but their presence in roots, where the functionality of structural support is questionable, might make this hypothesis untenable. Yet, roots in epiphytes do clasp supporting structures. Deterrence to insects and other predators has been offered as a function, but there is no supporting evidence.

That silica enters the plant body is a given fact, as the soil is rich in dissolved silicon and the atmosphere is also laden with particulate silicon. However, terrestrial orchids generally lack sclerenchyma and stegmata in their leaves and stems (Stern, 1993, 1997a,b) despite the availability of dissolved silicon. That silica is deposited along fibres is possibly a function of the proximity of vascular tissue to sclerenchyma. Still, the mysteriousness of stegmatal function remains.

Tilosomes, or rod bodies, Stabkörper, or fibre bodies, Faserkörper, of the German literature are characteristic of certain groups of orchids (Pridgeon, Stern & Benzing, 1983; Pridgeon, 1987). These are masses of cellulosic and/or ligneous material superadjacent in the velamen to passage cells of the exodermis. Tilosomes have several forms thought to be systematically significant in orchids, and certain taxa are characterized by them. They presumably function as absorbing structures to increase the effectiveness of passage cells, or perhaps are selective of the materials passing through the velamen and exodermis into the cortex. Tilosomes in Maxillarieae occur only in Lycastinae and Maxillariinae. Holtzmeier et al. (1998) show tilosomes in species of Maxillaria, Mormolyca and Trigonidium (Maxillariinae) they studied.

Foliar glands and fibre bundles occur principally in Lycastinae and Anthosiphon, Cryptocentrum and Cyrtidiorchis of Maxillariinae. Foliar glands also occur in Maxillaria, Mormolyca and Trigonidium (Holtzmeier et al., 1998). Similarly, foliar fibre bundles occur largely in Lycastinae and Anthosiphon and Cryptocentrum of Maxillariinae. However, Zygopetalum crinitum and Zygopetalum intermedium have fibre bundles, but other species of Zygopetalum do not; Scuticaria shows fibre bundles. Holtzmeier et al. (1998) demonstrated fibre bundles in leaves of Maxillaria, Mormolyca and Trigonidium.

Endodermal cell walls are U-thickened in most Zygopetalinae, O-thickened in most Lycastinae, Ornithocephalinae and Telipogoninae. They are thin-walled in Cryptarrhena lunata, Paradisianthus micranthus, Neomoorea wallisii and Rudolphiella floribunda. Among Zygopetalinae, Bollea violacea, Koellensteinia altissima and Warrea warreana have O-thickened endodermal cell walls. Pericycle cells are O-thickened throughout. In Maxillaria and Mormolyca, endodermal cells are mostly U-thickened; O-thickened in Trigonidium (Holtzmeier et al., 1998).

Most Zygopetalinae have plain-walled water-storage cells (Table 5) in mesophyll tissues. Pescatoria and Promenaea, by contrast, show water-storage cells with cell wall banding. Water-storage cells are absent in Aganisia, Kefersteinia, Neogardneria, Otostylis, Pabstia and Warrea. Water-storage cells are lacking in Lycastinae, but they are present in the mesophyll and hypodermis of Maxillariinae (Holtzmeier et al., 1998). In Ornithocephalinae, water-storage cells with banded walls are present, and in Telipogoninae plain-walled water-storage cells occur.

There is close anatomical agreement between Lycastinae and Maxillariinae in terms of the presence of stigmata, tilosomes, foliar glands, fibre bundles and O thickened endodermal cell walls, all of which are present in these taxa. Maxillaria and Mormolyca diverge in their U-thickened endodermal cell walls. Mesophyll in Lycastinae does not have water-storage cells, but these are present in Maxillariinae. Zygopetalinae are distant from these two taxa in their lack of tilosomes, foliar glands, foliar fibre bundles and U-thickened endodermal cell walls. Similarly, except for the presence of O-thickened endodermal cell walls, Ornithocephalinae and

Telopogoninae diverge anatomically from Lycastinae and Maxillariinae, but there is considerable agreement between the former two taxa.

CLADISTICS

Implicit enumeration and heuristic analyses of eight potentially phylogenetically informative characters (Tables 3, 4) resulted in the generation of 3509+ equally parsimonious trees of 20 steps, a consistency index (CI) of 0.45, and a retention index (RI) of 0.74, producing only one weakly supported hypothesis of phylogenetic relationship among these genera. The strict consensus of these cladograms is totally unresolved, suggesting that anatomical characters alone are of limited value in assessing relationships within Maxillarieae. Anatomical characters were also found to be quite homoplasious in the studies of Pridgeon & Chase (1995), Stern & Whitten (1999) and Stern & Judd (2001).

Although the strict consensus tree was totally unresolved, inspection of the numerous equally parsimonious trees resulting from the analyses revealed that all trees contained a clade that grouped *Anguloa*, *Bifrenaria*, *Cryptocentrum*, *Cryptidiorchis*, *Lycaste*, *Rudolfiella*, *Stenocoryne*, *Teuscheria* and *Xylobium* (sometimes along with various other genera). The collapse of this clade in the strict consensus tree results from the variable positioning of several genera, e.g. *Aganisia*, *Neogardneria* and *Otostylis*. The Maxillariinae + Lycastinae clade is supported by the presence of foliar glands (character #5).

Our results are in agreement with the detailed and ongoing molecular analyses of Williams et al. (1999) in that they support (albeit weakly) a phylogenetic relationship between Lycastinae and Maxillariinae. In fact, in our analyses, genera representative of these two tribes are intermixed within a single clade (in many of the most parsimonious trees), and this clade is diagnosed by the presence of foliar glands (Tables 3, 4). We find no anatomical character consistently distinguishing these two subtribes. Likewise, in preliminary DNA-based cladograms (Williams et al., 1999) Lycastinae are not resolved as monophyletic. Williams et al. (1999) therefore proposed an expansion of the circumscription of Maxillariinae to include Lycastinae. Our anatomical data support this taxonomic change.

Finally, the genera *Ackermania*, *Chaubardia*, *Chaubardiella*, *Chondrorhyncha*, *Cochleanthes*, *Dichaea*, *Huntleya*, *Pescatoria* and *Stenia* may be related because they are not differentiable on the basis of the anatomical characters included in our analyses. In the DNA-based phylogenetic analyses of Williams et al. (1999) all of these genera are members of a derived clade within *Zygopetalinae*, and this specialized clade is also unified by the loss of pseudobulbs.

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